F. L. FARQUHARSON

DEPARTMENT OF NATURE CONSERVATION, TRANSVAAL PROVINCIAL ADMINISTRATION WRITTEN WHILE AN OFFICER OF THE NATAL PARKS, GAME AND FISH PRESERVATION BOARD.

The distribution of cyprinids in South Africa

The most characteristic feature of the freshwater fishes in Southern Africa is the surprising reduction in the number of families represented in central and eastern Africa. The dominant family in southern Africa is the Cyprinidae. This family is represented by the genera *Labeo*, *Varicorhinus*, *Barbus*, *Barilius* and *Engraulicypris*, none of which is endemic to the region. Of these genera, *Varicorhinus* is of doubtful status while *Barilius* and *Engraulicypris* are probably each represented by single species.

In southern Africa, some groups of the Cyprinidae show a surprising degree of endemism whereas other groups have a very widespread distribution. This paper is an attempt to group the various Cyprinids of the region, to give a general account of their distribution and to give possible explanations to the problems posed by such distribution.

Acknowledgements

I am most grateful to Mr. R. S. Crass and Dr. J. C. Poynton for their valuable information, suggestions, criticism and encouragement.

I am indebted to the Director of the Natal Parks, Game and Fish Preservation Board, Col. J. Vincent, for the facilities provided while employed in his Department, to the Officers of that Board who assisted in the collection of material, to Mr. R. A. Jubb for valuable information on the distribution of various species, to Professor S. F. Bush and other members of the University of Natal who have supplied valuable information, and to the Directors and Staff of the South African and Natal Museums for making available material and records.

In this paper taxonomically related species have been aggregated into provisional groups (A to L) and are listed below. As the synonymy of the various species is extremely involved, the respective synonyms have not been listed with the species cited.

Group A *Labeo* in which the inner surface of the lips do not bear transverse plicae.

	Lateral line Scales	*Caudal peduncle Scales*
L. altivelis	36–39	16–18
L. rosae	37–40	18–20
L. tenuirostris	40–42	18–20
L. rubromaculatus	41–45	20–24
L. capensis	47–50	20–24
L. umbratus	57–65	30–34
L. quathlambae	65–68	30–34
? *L. seeberi*	82–90	36–50

Ann. Cape Prov. Mus. II. 1962. South Africa.

Group B *Labeo* which do bear transverse plicae on the lips.

L. forskalii	37–42	16–20
L. congoro	38–40	16–18
L. cylindricus	38–39	18–20
L. darlingi	36–39	16–20
L. rubropunctatus	36–39	18–20

Group C *Barbus* in which the scales are small and longitudinally striated.

B. natalensis	33–34	16–18
B. holubi	38–41	16
B. kimberleyensis	37–45	16
B. capensis	41–45	16–18

Group D *Barbus* (and *Varicorhinus*) in which the scales are large and longitudinally striated.

B. marequensis	27–34	12–14
V. nelspruitensis	36–40	14
V. pungweensis	28–30	12

Group E *Barbus* in which the scales are radiately striated, possessing a serrated dorsal spine and in which the adults attain at least 20 cms. standard length.

B. mattozi	33	14
B. rapax	29–35	14
B. andrewi	38–40	16
B. serra	41–44	20

Group F *Barbus* in which the scales are small and radiately striated, possessing a serrated dorsal spine and in which adults seldom attain more than 10 cms. standard length.

B. paludinosus	32–36	16–18
B. hospes	37–39	16
B. calidus	34–38	14
B. trevelyani	33–36	14
B. ivongoensis	34	14
B. afrohamiltoni	29–34	16
B. argenteus	27–33	14

Group G *Barbus* in which the scales are large and radiately striated, possessing a serrated dorsal spine, and adults seldom attaining more than 10 cms. standard length.

B. eutaenia	24–27	12–14
B. multilineatus	25–27	10–12
B. afrovernayi	27–29	12
B. kessleri	24–26	12
B. tangandensis	22–24	12

Group H *Barbus* in which the scales are radiately striated and in which the dorsal spine is not serrated.

B. trimaculatus	30–35	14–16
B. bernardcarpi	31–35	14

GROUP I *Barbus* in which the scales are small and radiately striated, and a true dorsal spine is lacking.

B. senticeps	30–34	12
B. burchelli	28–36	12
B. phlegethon	30–36	12
B. tenuis	32–36	12–14
B. vulneratus	33–36	12–14
B. asper	34–38	14–18
B. anoplus	32–36	14–16
B. labialis	33–37	16
B. gurneyi	31–35	12–14
B. inermoides	35	12

GROUP J *Barbus* in which the scales are large and radiately striated, and a true dorsal spine is lacking.

B. viviparus	28–31	12
B. thamalakanensis	25–28	12
B. lineomaculatus	27–32	12
B. puellus	27	12
B. rubellus	24–26	12
B. treurensis	26–30	12
B. barotseensis	26–29	12
B. radiatus	26–27	12
B. toppini	27–28	12
B. pallidus	27–30	12
B. annectens	27–29	12
B. barilioides	28–30	12
B. fasciolatus	25	12
B. palustris	26–28	12
B. aurantiacus	26–28	12

GROUP K *Barilius* species.
Only one species in the area.
B. zambesensis

GROUP L *Engraulicypris* species.
E. brevianalis, E. gariepinus and *E. whitei.*

DISTRIBUTION

Genus *Labeo:* Groups A and B.

There are at present 13 recognised species in southern Africa.

GROUP A (Fig. 1)

Of this group, *L. capensis* and *L. umbratus* share the Orange System, but the latter, possibly through catchment exchange, has gained access to the southern Cape watershed. A species closely related to *L. capensis* is *L. rubromaculatus*, found only in the Tugela System. *L. quathlambae*, apparently related to *L. umbratus*, is found in the upper Umkomazana River. Both these Natal fishes undoubtedly gained access to their respective localities through catchment exchange high in the Drakensberg. The Limpopo System has two species of this group, *L. tenuirostris* and *L. rosae*, of which the latter extends southward to the Pongolo River. To the North, the group is represented by *L. altivelis*, from the Zambezi to the Sabi-Lundi Rivers. *L. seeberi* from the Olifants River of the South Western Cape has been assigned to this group following information from Mr. R. A. Jubb (unpublished).

The general picture of this group is an almost continuous distribution from the Zambezi to the Cape. The degree of speciation and the southern limits of this group suggest a relatively old dispersion.

GROUP B (Fig. 2)

In this group *L. cylindricus*, *L. darlingi*, *L. congoro* and *L. forskalii* are found in the Zambezi, however the latter apparently replaces the former above the Victoria Falls. *L. cylindricus* extends southward to the Pongolo River while *L. darlingi* extends a little farther south to the Tugela River. *L. rubropunctatus* is the only species of this group not found in

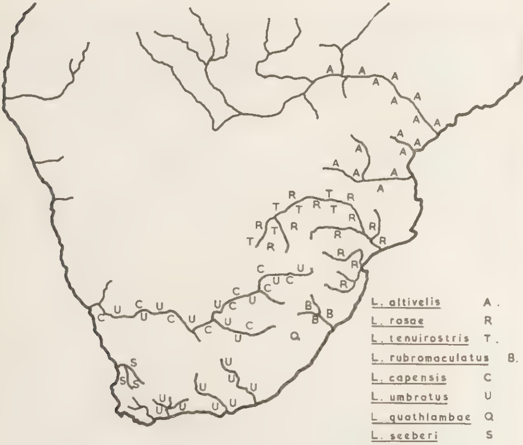


Figure 1. Group A.

the Zambezi and its distribution is from the Limpopo southward to the Pongolo River.

This group is probably of a more recent dispersion than group A as, apart from a smaller degree of speciation and endemism, it has not extended as far southward.

Genus *Varicorhinus*. The Southern African representatives of this genus closely resemble species of the genus *Barbus* and the only character separating these genera is qualitative. Unfortunately this problem of systematics cannot be dealt with here so for the purposes of this paper the two species of *Varicorhinus* are listed as distinct species in group D.

Genus *Barbus:* Groups C to J inclusive.

Forty-eight species of this genus have been listed in this paper but as there is still some taxonomic confusion in this genus it is likely that a number of these species will become synonyms in the future.

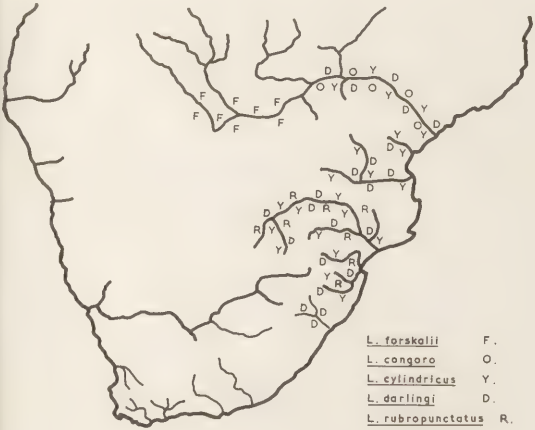


Figure 2. Group B.

GROUP C (Fig. 3)

B. natalensis occurs in the Limpopo and all East-flowing rivers southward to the Umtamvuna. Two species, *B. kimberleyensis* and *B. holubi* are endemic to the Vaal–Orange System. *B. capensis* is endemic to the Olifants River of the South Western Cape.

Although this group appears to be absent from North of the Limpopo River to the Zambezi, it is represented in Central Africa and elsewhere. The endemism and widespread distribution probably indicates an old dispersion possibly contemporaneous with that of group A.

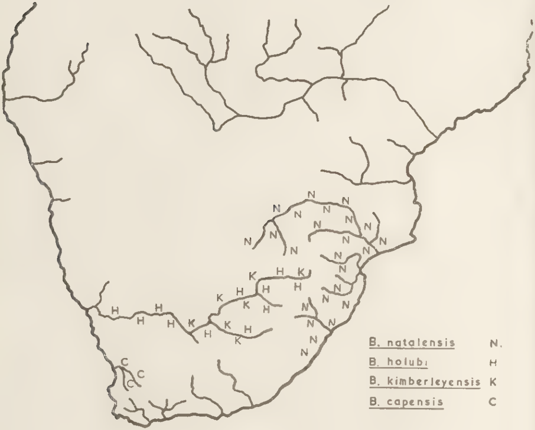


Figure 3. Group C.

GROUP D (Fig. 4)

B. marequensis is found in all East-flowing rivers from the Zambezi to the Pongolo. *V. pungweensis* is found, as the name suggests, in the Pungwe River and *V. nelspruitensis* occurs in the Incomati and Pongolo-Usutu Systems.

As no members of this group are to be found in the Orange System or South of the Pongolo River, it is suggested that the dispersion of this group is fairly recent, possibly occurring at the same time as that of group B.

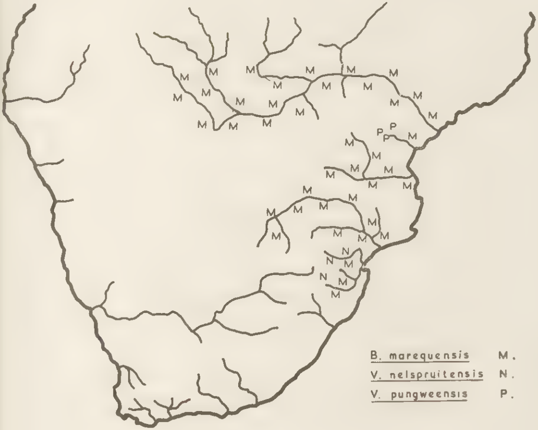


Figure 4. Group D.

GROUP E (Fig. 5)

B. mattozi occurs in the upper reaches of the Zambezi System. *B. rapax* is found in certain sections of the Limpopo and its tributaries. *B. andrewi* and *B. serra* are found in the South-western Cape area, the former in the Berg and Breede Rivers and the latter in the Olifants River.

Apart from the geographic isolation of the members of this group, it is interesting to note that there are no records of the group between the Zambezi and North Africa where it is again represented. The dispersion of this group probably dates to that of group A and C or perhaps even earlier.

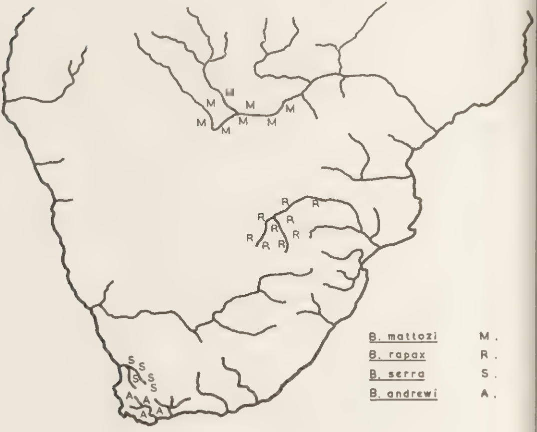


Figure 5. Group E.

GROUP F (Fig. 6)

The distribution of this group is particularly interesting as it seems to indicate two separate phases of dispersion. The earlier dispersion gave rise to a number of endemic species at more or less isolated localities in southern Africa. *B. hospes* is endemic to the lower Orange River and *B. callidus* to the Olifants River. On the east coast, *B. trevelyani* is to be found in a few rivers around the King William's Town area, *B. ivongoensis* in the Ivongo River (Natal South Coast) and *B. afrohamiltoni* is found from the Pongolo to the Sabi-Lundi System. *B. argenteus* is known from the Incomati and Pongolo Rivers but has also been recorded from the Kunene River. The second or later phase of dispersion brought about the widespread distribution of *B. paludinosus*, from the Zambezi and Kunene Rivers in the north of the region to the Orange on the west coast and the Umhloti River (Natal) on the east coast.

The earlier phase of dispersion may have occurred along with those of groups A, C and E, while the later phase probably dates with those of groups B and D.

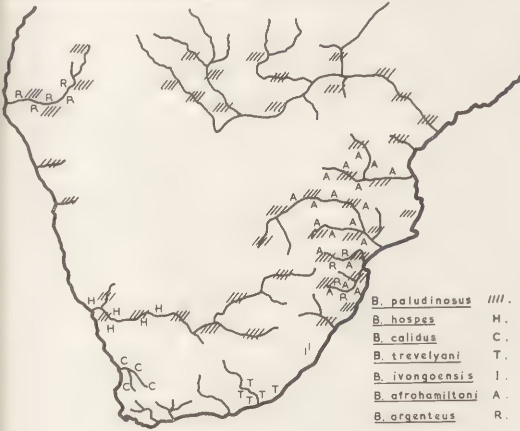


Figure 6. Group F.

GROUP G (Fig. 7)

B. eutaenia is found from the Zambezi and Kunene Rivers southward to the Limpopo River. This species may be synonymous with *B. kerstenii* from East Africa. *B. tangandensis* is found in the upper Zambezi, *B. multilineatus* and *B. afrovernayi* in the middle Zambezi, but the latter has also been recorded from the Kunene River. *B. kessleri* is found around the Beira area.

It may be that this group also shows two phases of dispersion with *B. eutaenia* representing the widespread form and regarding the other species as relicts, but further information is required on this group. Assuming two phases to have occurred, the tentative dating would be similar to that of group F.

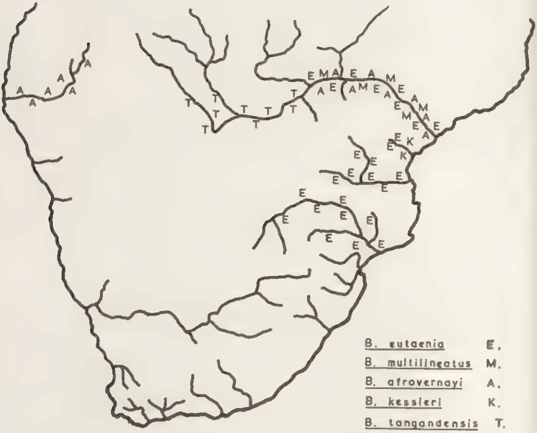


Figure 7. Group G.

GROUP H (Fig. 8)

This group is represented in the area by only two species, *B. bernardcarpi* in the upper Zambezi and Okovango areas and *B. trimaculatus* from the Zambezi and Kunene Rivers southward to the Tugela River in the east and to the Vaal River but apparently not the Orange River in the west.

The dispersion of this group occurred probably at the same time as that of groups B and D.

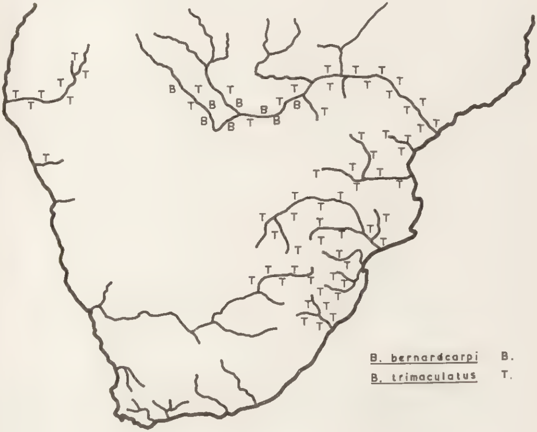


Figure 8. Group H.

GROUP I (Fig. 9)

This group, like group F, is characterised by having a widely distributed species, *B. anoplus* and a large number of very localized species. *B. anoplus* is found probably from the Incomati system southward to the Great Fish River of the eastern Cape and also in the Orange-Vaal System. It appears to have gained access from the latter to the Gouritz System and the Olifants River. *B. senticeps* is found in the Zwartkops and Kromme Rivers, *B. tenuis* in the Gouritz River, *B. burchelli* in the Berg and Eerste Rivers, *B. phlegethon* in the Olifants River, *B. vulneratus* in the Breede River, *B. asper* in the Gouritz to the Gamtoos River, *B. labialis* in the Limpopo System, *B. inermoides* in the Kunene River, and *B. gurneyi* from the Umtamvuna River northwards to the Incomati System.

It seems likely that this is another group with two phases of dispersion, the earlier phase probably occurring along with that of group E, but it is difficult to date with any degree of

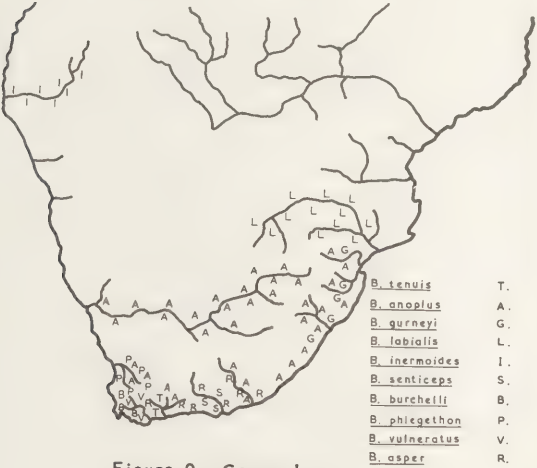


Figure 9. Group I.

accuracy the dispersion of *B. anoplus* owing to the fact that the group is apparently not represented in the Zambezi System nor in the rivers southward to the Limpopo, and also because of the fact of its presence in the Olifants River of the south-western Cape.

GROUP J (Fig. 10)

Due to the synonymy, the apparent randomness of distribution and the confusion of names, individual species localities will not be cited, but reference should be made to figure 10.

As a whole the group extends from about Port Elizabeth northwards to beyond the Zambezi System and is also represented in the Vaal and Kunene Rivers and in the Okovango area. Little can be said about the dispersal of this group until the systematics are further worked out and more precise data is available. It is however probably yet another group showing a twofold dispersion with *B. viviparus* as the widespread species.

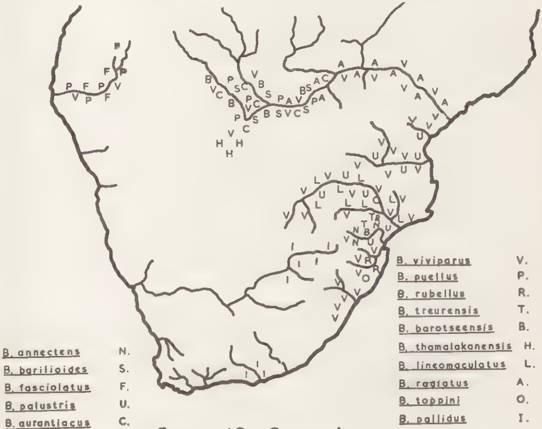


Figure 10. Group J.

Genus *Barilius*

Group K (Fig. 11)

The genus *Barilius* is represented in Southern Africa by probably only a single species, *B. zambesensis*. The distribution of this species extends from the Zambezi southwards to the Pongolo River. Its dispersion probably occurred about the same time as that of groups B and D.

Genus *Engraulicypris*

Group L (Fig. 11)

Three species of this genus have been recorded from Southern Africa; *E. brevianalis* from the Dwaars River (Transvaal) and from the Pongolo to the Umfolozi Rivers in Natal; *E. whitei* from the Limpopo System; and *E. gariepinus* from the Orange River. All three species are highly variable and it seems probable that only one or perhaps two species will be recognised in the region when material from sufficient localities is compared.

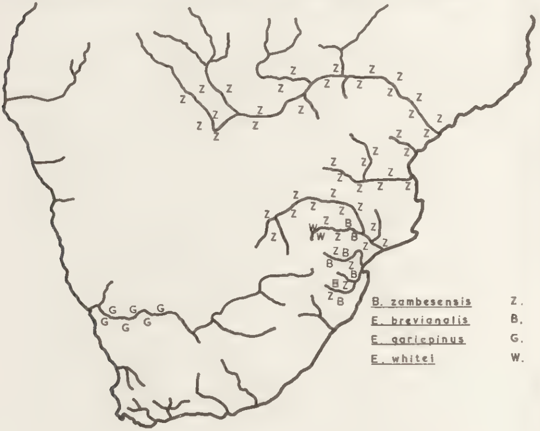


Figure 11. Groups K & L.

Discussion

The Influence of Water Temperature on Scale Formation

Barnard makes reference to Mottley (*Fishing Gazette* cxv, No. 3155, Oct. 1937) who found that the number of scales in North American trout is dependent on the temperature at the eyed-egg stage and for about five weeks thereafter: the higher the temperature the lower the scale-count. Although water temperature data are not available as yet, it is interesting to note the variation in scale count in groups A and E when the species are arranged in order of localities—approximately from "hot" to "cold".

Table I

Group A

Species	*Locality*	*Lateral Line Scales*
L. altivelis	Zambezi	36–39
L. rosae	Limpopo—Pongolo	38–40
L. tenuirostris	Upper Limpopo	40–42
L. rubromaculatus	Tugela	41–45
L. capensis	Orange	47–50
L. umbratus	Orange and S. Cape	57–65
L. quathlambae	Upper Umkomazana	65–68
L. seeberi	Olifants	82–90

Group E

Species	*Locality*	*Lateral Line Scales*
B. mattozi	Zambezi	33
B. rapax	Limpopo	29–35
B. andrewi	Berg and Breede	38–40
B. serra	Olifants	41–44

Although practically nothing is known of the breeding habits of these species, it seems probable that these figures are a further corroboration of Mottley's findings. I do not suggest that the species within the two groups are synonymous but only that they share recent common ancestry.

Apparently converse to the above findings, *Barbus natalensis* shows a reverse correlation of scale-count to water temperatures. Table 2 gives the average lateral line scale counts of this species from Natal and the Transvaal in a north to south sequence.

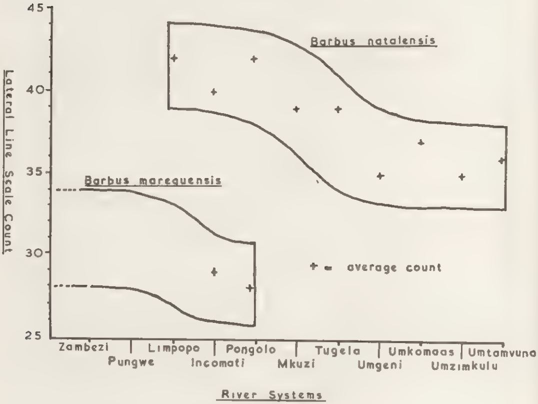
Table 2

Lateral Line Scale-counts in *Barbus natalensis*

River		*Lateral Line Count*
Limpopo	(Marico River)	42 average
Incomati	(Komati River)	40 ,,
Pongolo-Usutu	(Usutu River)	42 ,,
Mkuzi River		39 ,,
Tugela River		39 ,,
Umgeni River		35 ,,
Umkomaas River		37 ,,
Umzimkulu River		35 ,,
Umtamvuna River		36 ,,

The picture in Table 2 is however complicated by the fact that the southern limit of distribution of *Barbus marequensis* occurs almost in the middle of the range of *B. natalensis*. Thus if the scale counts of the one species are plotted with those of the other as in Table 3, the correlation with water-temperature becomes less significant.

TABLE 3



Lateral Line Scale-Count

My interpretation of this north/south variation in scale-counts lies in the theory of divergence of species.

Assuming that *Barbus natalensis* occurred in its present distribution originally with a range in the lateral line scale count of from 35 to 39, and that *B. marequensis* was a later invader with a count of from 28 to 34, the theory of divergence of species would suggest that where the two species occurred together a divergence of characters common to both would take place in time.

The evidence in Table 3, I believe, supports the above assumptions and hypothesis but further work on other characters will have to be undertaken before confirmation.

Dispersal

Cyprinids are known as Eocene fossils in Europe and as Miocene fossils in North America but no references to Tertiary fossil Cyprinids could be found from southern Africa.

As this family is found exclusively in fresh water (classified by Myers as a First Order fresh-water fishes), how did they get to their present localities?

Various hypotheses have been put forward to explain this question the most important of these being:

(1) Transport of young fish or eggs on the legs of birds, e.g. ducks and waders;
(2) Exchange of river catchments;
(3) Reversal of flow in rivers by continental tilting;
(4) Pluvial periods;
(5) Submergence and emergence of coastlines.

Of the above hypotheses, (1) is of minor importance unless the two river systems were in close proximity and if so it is more probable that (2) would account for the dispersion. It is however unlikely that (2) could account for the colonization of the whole of southern Africa. There appears to be little evidence for (3) in southern Africa. Pluvial periods and rise and fall of the coastline are discussed in more detail below.

Pluvial Periods and Geological Evidence

Although Pluvials are known to have occurred in Central and East Africa there appears to be little evidence for such occurrences in southern Africa. Kokot (1948) maintains that since the Pleistocene there has been a dry Kalahari Period followed by the return of more humid conditions, and he discounts any idea of pluvials during the latter period in this region: ". . . at no stage was the rainfall much more than it is now for any great length of time". Against this, Janmart has found in Angola three separate stages of Kalahari Sands interspersed with fluviatile deposits dating from the Middle and Upper Pleistocene. At the Victoria Falls, Clark has demonstrated a series of Kalahari-type Sands alternating with fluviatile deposits of the same date, and similar deposits have also been found on the Vaal River.

Cooke (1959) is of the opinion that the stratification mentioned above indicates very dry intervals rather than very wet periods, and that author, working on the structure of the sand particles also dates these periods as Middle and Late Pleistocene.

Thus according to the geologists the Early Pleistocene was an extremely dry phase followed by a return to conditions not unlike the present, but interspersed with further dry periods. Such fluctuations in conditions would undoubtedly result in considerable erosion and so the hypothesis of catchment exchange as a means of dispersal becomes more significant.

Submergence and Emergence of Coastlines

According to Barnard, the Breede, Gouritz and Gamtoos Rivers each have their own characteristic fish fauna and also contain the remnants of Cretaceous beds. As the genus *Barbus* is not known from pre-Tertiary times, the fish must have entered well after the establishment of these rivers.

Du Toit and Krige consider the extended Breede to have joined the extended Gouritz before the resubmergence of the Agulhas Bank in the Late Pleistocene, but according to Barnard the fish faunas of the two rivers are totally different. Hence these rivers must either have been populated before the Late Pleistocene and become differentiated since then, or they were never joined. Barnard regards the latter conclusion as the more plausible.

The rise and fall of the eastern coastline of Africa could account for the southerly dispersion of many species. There is little doubt that the Limpopo, Incomati and Pongolo-

Usutu Systems were joined in the past and they may also have been joined by a southerly extension of the Zambezi.

From the Tugela River northward to the Zambezi there is an ever widening low lying coastal plain considerable portions of which become inundated in the rainy season giving fish access from one area to another. Through Natal and Pondoland the coastal shelf becomes very narrow and the coastline steeper, making access from one river to another increasingly difficult —in fact there is only one Cyprinid, *Barbus anoplus*, whose distribution range extends southward through the rivers of Pondoland into the Cape proper. Another curious feature of this fish is that it is the only species that is present in the Olifants River (S. W. Cape) that is not endemic to that river.

I have suggested earlier in this paper that there have been two or more "waves" of Cyprinid dispersal in Southern Africa. The wet and dry periods during the Pleistocene were a somewhat cyclic occurrence as also appears to be the rise and fall of the coastline. These in themselves would suggest alternating periods whereby the fishes could move from one area to another. The evidence from the distribution patterns of the various groups, and in some the combination of "relict" endemics and a single wide-spread species, further confirms this.

That there have been two Cyprinid "invasions" during the Pleistocene seems probable, but the existence of present species prior to that time is uncertain. The fishes of the Olifants River (S. W. Cape) Cyprinids and other families represented, suggest perhaps an earlier origin.

CONCLUSIONS

Southern Africa has been subject to a series of Cyprinid invasions. The remnants of the earlier invasions have become isolated in the various river systems and have undergone speciation to a greater or lesser extent. Later invaders have ousted some of their predecessors in many systems thus giving the relict fauna its characteristic discontinuous distribution.

There appears to be nothing in southern African rivers which could account for their not being colonized by Cyprinids. The only factor preventing such distribution appears to be the accessibility of rivers to the fish.

Rise and fall of the coastline and exchange of river catchments during the Pleistocene appear to be the main factors in dispersal. Factors accounting for dispersal, occurring in a cyclic manner, have given rise to a wave form of dispersion.

BIBLIOGRAPHY

BARNARD, K. H. 1943. *Ann. S. Afr. Mus.* 36: 101-262.

COOKE, H. B. S. 1957. *Trans. Geol. Soc. S. Afr.* annex. to 60.

KOKOT, D. F. 1948 An investigation into evidence bearing on recent climatic changes over Southern Africa. Irrigation Dept. Memoir. Pretoria.

DISCUSSION

Dr. Macnae: Except at the Zambezi mouth, the continental shelf of the east coast of southern Africa is rather narrow, varying from about two to five miles in extent. I suggest, that this is insufficient to support the idea that a rising and falling coastline can have afforded much aid to distribution.

Mr. Farquharson: The coastline is steepest in the Pondoland area and it is interesting that that region has only one species.

Dr. Talbot: Although it seems fairly reasonable to assume that there may have been a series of two or more Cyprinid invasions in southern Africa, I think that the patterns of distribution here described could also arise in other ways. The existence of a single widespread species in several of the groups is not really proof of "wave" invasion.

Dr. Winterbottom: I am not sure whether Dr. Talbot is right. In the presence of a single widespread species, it is difficult to know how other species could develop unless they all arrived in the area in a series of different waves.

Prof. Ewer: Lack has emphasized Gause's principle which states that when two closely related species occupy the same habitat they must be ecologically differentiated if one is not to eliminate the other through competition. This seems to support Dr. Talbot.

Dr. Winterbottom: I think this raises an entirely different question. Is there any evidence of ecological isolation between the clusters of related species which occur in the lakes?

Mr. Farquharson: All the endemic species are physically isolated, each being peculiar to an isolated river system. In the lakes, differences in breeding behaviour appear to be the main isolating factors.

Mr. Grindley: In the Cape we appear to have a relict of a paleogenic fauna in *Galaxias*.

Mr. Farquharson: These fish, rather like trout, are probably of marine origin and there is no good evidence that they are paleogenic.

Dr. McLachlan: Have the Cyprinids any tolerance of salinity? I ask because there is often seepage into the areas behind coastal dunes forming pools and lagoons which may be more or less salty or fresh. These may afford a pathway between river systems.

Dr. Stuckenberg: I have investigated some of the insects inhabiting such pools, and have found them all widespread, unspecialized forms.

Mr. Farquharson: Salt tolerance in Cyprinids is probably low.

Prof. Ewer: Do you base this on observations or experimental measurements?

Mr. Farquharson: On the observation that they do not occur near estuaries.

Mr. Liversidge: *Barbus* does occur in the lower more saline reaches of the Olifants River, but it is rare.

Dr. Harrison: We found *Barbus* in the estuary of the Olifants River only after floods which had pushed the salt water right out of the lagoon.

Prof. Ewer: Here again we must distinguish between habitual selection and tolerance. The point is that although the fish might not generally choose to live in saline estuaries they *could* use these conditions to move from one river to another.

Mr. Liversidge: During floods in the eastern Cape, fresh water from the Sundays River actually flowed along the coast to well beyond the Bushmans River mouth. It is thus conceivable that fish might get from one to the other with only a small degree of salt tolerance.

Dr. Harrison: This is a very good point and worth further investigation. At False Bay, St. Lucia for instance, we found many skulls of *Clarias* which had apparently come down river and died, but we found no remains of *Barbus*.